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SHELL SHAPE DIFFERENCES BETWEEN TWO *PANOPEA* SPECIES AND PHENOTYPIC VARIATION AMONG *P. GLOBOSA* AT DIFFERENT SITES USING TWO GEOMETRIC MORPHOMETRICS APPROACHES

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ABSTRACT

Most previous studies identifying *Panopea generosa* and *P. globosa* have used non-rigorous visual methods as well as older shell measurement techniques. Newer mathematical methods based on shell shape variation allow for more accurate identification of clam species, as well as modeling of phenotypic differences due to environmental effects in populations in different sites. Interspecific shell morphology for two Mexican geoduck clam species was analyzed from a total of five sites off both coasts of the Baja California peninsula. In addition, intraspecific analyses of shell morphology were conducted for one of the species, *P. globosa,* at four sites along its reported distribution. Two approaches were employed for the analyses: a novel approach based on radiating lines to characterize shell outlines, and a more traditional approach using internal shell landmarks. In general, the novel approach afforded greater fidelity in distinguishing inter- and intraspecific variation. Our results from both methods agree with original species descriptions, and showed that Bahía Magdalena geoducks are *P. globosa*, thus revealing a wider distribution than previous reports for this species. The outline and internal scars were highly discriminant between the two species. Shell shape of *P. generosa* was also less variable than that of *P. globosa*. Intraspecific analyses of *P. globosa* shell shape suggest an adaptive or phenotypic response to environmental conditions at each site. Our results may also be indicative of reproductive isolation between Pacific *P. globosa* at Bahía Magdalena and conspecifics in the Gulf of California.

Key words: *Panopea*, geoduck, shape differences, geometric morphometrics.

INTRODUCTION

Mollusks of the genus *Panopea* include among the largest of all deep-burrowing bivalves, with congeners occurring worldwide in intertidal and subtidal regions in the Pacific and Atlantic Oceans, the Mediterranean Sea, as well as off the coasts of Australia and New Zealand (Yonge, 1971). Two *Panopea* species, *P. generosa* (Gould, 1850) and *P. globosa* (Dall, 1898), commonly called the “geoduck clam”, occur in coastal waters of the Baja California Peninsula in both the Pacific Ocean and the Gulf of California.

Some authors report *P. generosa* distributions from south of Alaska to the Baja California peninsula (Weymouth, 1921; Fitch, 1952; Moore, 1968; Morris et al., 1980; Goodwin & Peace, 1989; Coan et al., 2000), whereas others include Baja California Sur (SAGARPA, 2007) and Gulf of California (DFO, 2000; Moore, 2001; Feldman et al., 2004; Demeré & Scott, 2006) within its distribution range. In contrast, the distribution of *P. globosa* has been reported as limited to the northern Gulf of California (Keen, 1971; Coan et al., 2000; Aragón-Noriega et al., 2007; Rocha-Olivares et al., 2010), although specimens were recently reported from the central eastern side of the Gulf of California off the mainland coast of Mexico near Guaymas, Sonora (Aragón-Noriega et

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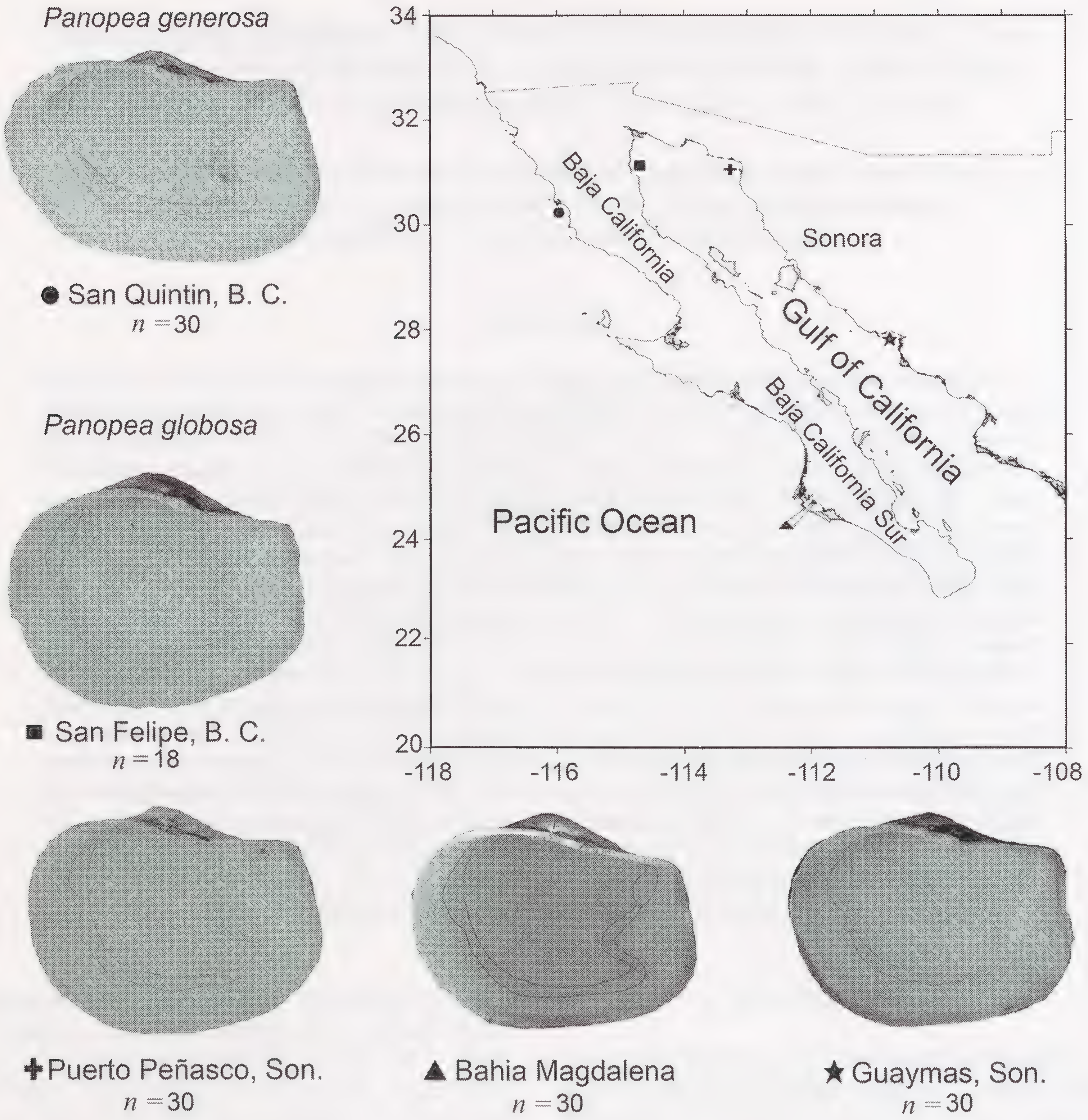

FIG. 1. Sampling sites of two *Panopea* species in northwest Mexico.

al., 2007), as well as the Pacific side of the Baja California peninsula in coastal waters of Bahía Magdalena (Fig. 1; González-Peláez, Centro de Investigaciones Biológicas del Noroeste, México 2010, pers. comm.).

Misidentifcation of *Panopea* species, on the other hand, remains a problem since morphometric plasticity is known to occur in the genus. For example, one case that is well documented is that of *Panopea generosa*, which had been mistakenly synonymized with the extinct *P. abrupta* for almost 25 years (Vadopalas et al., 2010).

Moreover, identification can be difficult because bivalve shell morphology is influenced by such environmental factors as temperature, tidal excursion, wave exposure, water currents and sediment type (Costa et al., 2008a). The marine environment along the peninsula and the Gulf of California is highly variable, with seasonal circulation patterns (Zaytsev et al., 2003; Kessler, 2006; Lavín & Marinone, 2003) and differences in bathymetry (Bray, 1988; Lluch-Cota et al., 2007) that may influence regional morphological changes in metapopulations (Helenes & Carreño, 1999; Bizzarro, 2008; Álvarez et al., 2009).

The relationship between local environmental conditions and shell morphology in *Panopea*

TABLE 1. Geoduck (*Panopea* spp.) sampling sites and number of specimens used for interspecific and intraspecific geometric morphometric analysis.

Locality	Abbreviation	Location	Specimens
San Quintín	SQ	30°23'N, 115°57'W	30
San Felipe	SF	31°01'N, 114°49'W	18
Puerto Peñasco	PP	31°18'N, 113°33'W	30
Guaymas	GU	27°56'N, 110°51'W	30
Bahía Magdalena	BM	24°39'N, 112°03'W	30

are unknown. Given the propensity for variability in valve shape due to regional environmental variation (Fyfe, 1984), characterizing the variation in shell morphology between and within *Panopea* species could allow for more accurate estimates of population distributions. Shell morphology and structural traits are the principal characters used in traditional taxonomy of bivalves, including *Panopea generosa* and *P. globosa.* The shell of adult *P. generosa* is heavy, ponderous, subquadrate, subequilateral and the valves gape widely (Coan et al., 2000; Vadopalas et al., 2010). By comparison, the shell of adult *P. globosa* is more inflated, expanded and rounded in the pedal region, with a narrower posterior end and non-parallel opposite margins (Dall, 1898). Fyfe (1984) described the shell morphology of *P. generosa* as highly variable and taxonomically difficult to identify using traditional morphometric data (length, depth, and width). Thus, morphological differences between congeners of *Panopea* and its conspecifics are often difficult to identify by inexperienced observers.

Because linear measurements can be fairly ambiguous (Zelditch et al., 2004), researchers have explored geometric methods as an alternative for quantifying and analyzing morphological variation. Some of the more promising methods include the use of points that fall at defined intervals along a curve between two distinct landmarks; Marko & Jackson (2001) termed these points semi-landmarks.

Geometric morphometrics in other taxa have been shown to be powerful tools for solving complex species-level identification problems (Matias et al., 2001; Gumiel et al., 2003; Shipunov & Bateman, 2005). Relatively few studies have applied these techniques to mollusks. Some focused on general morphology (Ubukata, 2003; Anderson & Roopnarine, 2005; Carvajal et al., 2005, 2006; Roopnarine et al., 2008), while others used geometric morphometrics to compared external shapes among conspecific populations (Kwon et al.,1999; Costa et al., 2008b) or phenotypic stocks (Márquez et al., 2010).

To help resolve the difficulty in species identification, which is affected by shell shape variation, we used two methods of geometric morphometric analyses to characterize shell shape differences in *Panopea* spp. from five sites on the Baja California peninsula. The first method is Procrustes superimposition which, to our knowledge, has not yet been used with bivalves. This newer method involves generating radiating lines, which fan out from a centroid and is referred to herein as "Fan-Based." The second method is based on anatomical landmarks of the inner shell.

MATERIALS AND METHODS

Samples and Sites

For taxonomic identification, we used the original descriptions (Conrad, 1849; Gould, 1850; Dall, 1898), recent identification keys (Keen et al., 1971; Coan et al., 2000) and the direct help of Paul Valentich-Scott (Curator of Malacology, Santa Barbara Museum of Natural History). Using SCUBA, divers collected adult *P. generosa* specimens from San Quintín (n = 30) and a total of 108 adult *P. globosa* specimens from San Felipe (n = 18), Puerto Peñasco (n = 30), Guaymas (n = 30) and Bahía Magdalena (n = 30; Table 1; Fig. 1).

Imaging and Measurement

The principles of the FB method are well described elsewhere (e.g., Sheets et al., 2006a; Rohlf, 1990; Lawing & Polly, 2009). For this

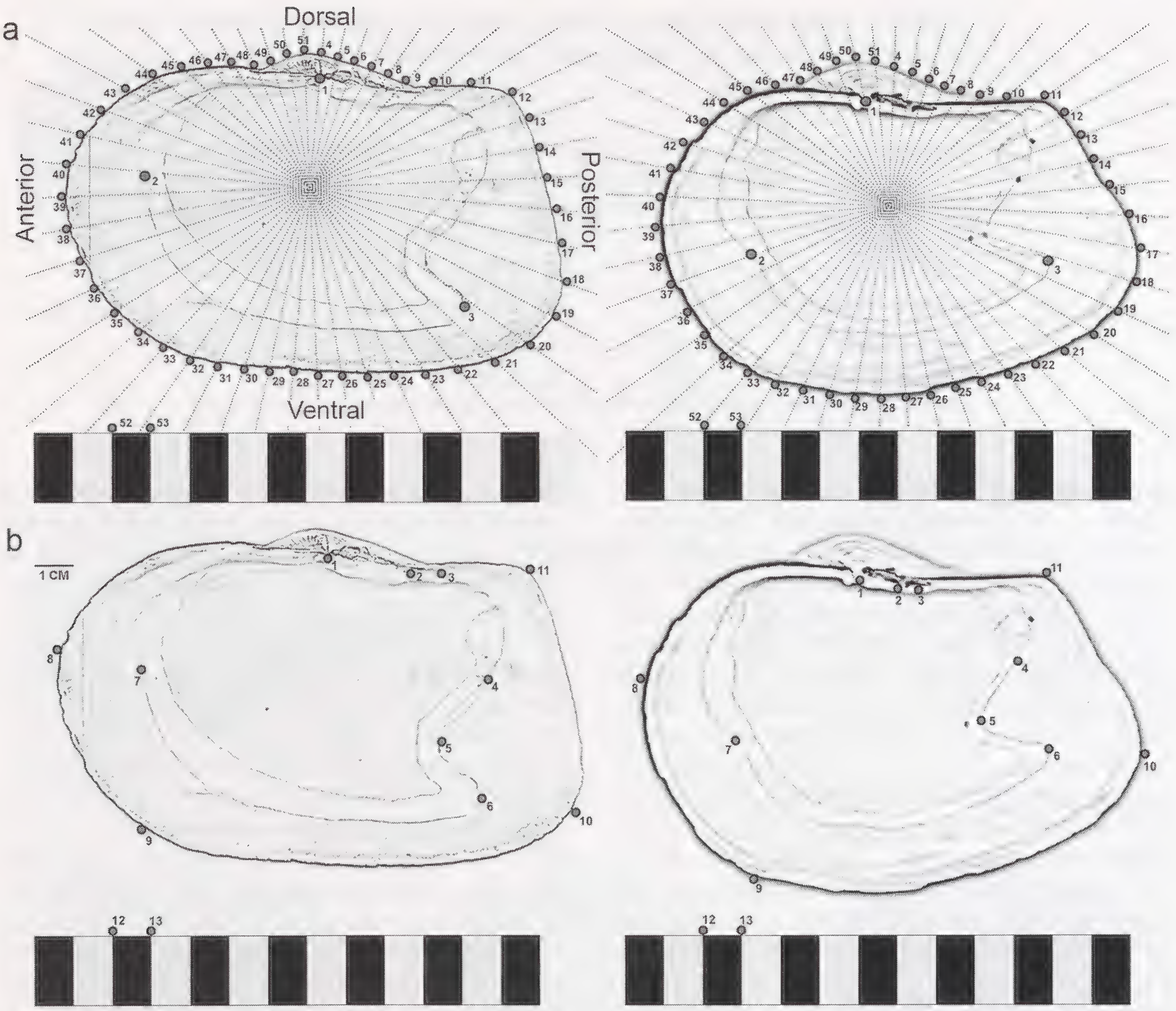

FIG. 2. Digitized landmarks and coordinates located for *Panopea generosa* (left) and *P. globosa* (right). Where (a) is the fan-based method showing the intercept between the valve contour and the drawing aligment fan (48 equal quadrants), and (b) is the internal scar method showing landmarks 1–3 which describe nymph shape while landmarks 4–6 describe the deep pallial sinus.

method, the set of points was defined *a priori* by an arbitrary rule: rays at equal angular intervals were used as guides to digitize semi-landmarks, with the points to be digitized located at the intersection of all radii of a circle and the outline curve (Sheets et al., 2006a; Rohlf, 1990; Lawing & Polly, 2009). As employed here, the FB method involved generating three anatomical landmarks and two-dimensional Cartesian coordinates of 48 semi-landmarks (Fig. 2a) using Makefan6 (Sheets et al., 2006b). We used these landmarks to align shapes via Procrustes superimposition. We used anatomical scars for landmarks 1, 2, and 3 (Fig. 2a) (umbo, antero-ventral adductor muscle, and postero-ventral pallial sinus) to determine centroid size, semi-landmarks 4 to 51 to analyze curves and shell shape variation (semi-landmarks 4–11 and 45–51 to define the dorsal region; 12–20 to define the posterior end; 21–33 to delineate the ventral region, and 34–44 to define the anterior end). We used marks 52 and 53 as a reference scale (tpsDig 2.12, Rohlf, 2008). We used Semiland v6 software (Sheets et al., 2006b) to conduct FB analyses.

The ILB method analyzed the interior shape of each specimen using 11 landmarks (Fig. 2b). We used landmarks 1–3 to analyze nymph shape; 4–6 to analyze pallial sinus depth; landmark 7 to characterize the antero-ventral adductor scar and landmarks 8–11 to define outline curves. As above, we used landmarks 12 and 13 as a reference scale (Fig. 2b; tpsDig 2.12, Rohlf, 2008). We translated the interior

TABLE 2. Variance explained by the first two principal components between *Panopea generosa* and *P. globosa* and within *P. globosa* groups.

	Group	PC I (in %)	PC II (in %)	Overall (in %)
Outline				
Interspecific	*P. generosa*	52	19	71
	P. globosa	36	30	66
Intraspecific	SF	48	15	53
	PP	35	22	57
	GU	41	25	66
	BM	43	28	71
Internal landmarks				
Interspecific	*P. generosa*	33	25	58
	P. globosa	28	17	45
Intraspecific	SF	34	14	48
	PP	31	19	50
	GU	35	16	51
	BM	33	21	54

landmark coordinates to align the centroids of each individual. To minimize least-squares differences between landmark alignments, we used CoordGen6f (Sheets et al., 2006b) to rotate and scale centroid size to unity, producing Procrustes shape coordinates and consensus shapes for each group.

Analyses of Interspecific and Intraspecific Variation

To determine differences in outline (FB method) and internal landmarks (ILB method) between *P. generosa* and *P. globosa*, we used CVAGen6m (Sheets et al., 2006b) to perform canonical variates analysis and multivariate analysis of variance (CVA–MANOVA). To assess within-group shape variation, we used PCAGen6n software (Sheets et al., 2006b) to perform principal component analysis (PCA). To determine which canonical variates (CV) were effective discriminators, we employed Bartlett's test based on Wilk's lambda (Λ), which is the within-groups sum of squares divided by the total sum of squares. A value of Λ near 0 (zero) indicates high discrimination between groups (Zelditch et al., 2004).

We assessed the statistical significance of shape differences using Goodall's F-test. We calculated the full and partial Procrustes distances between means (DBM) of two groups and bootstrapped to estimate the variance of this distance using TwoGroup6A software (Sheets et al., 2006b). We employed Mahalanobis distances (Mahalanobis, 1936) to determine the probability that the distance between an individual and the mean of the group was larger than expected under the null model of random variation around the mean of each group (Zelditch et al., 2004).

To visualize the shapes, we used thin-plate splines of the first two principal components. Thin plate splines provide graphical representations of the deformation of a square grid based on the difference in position of individual landmarks and displacement of the vectors relative to a grand mean consensus form (Bookstein, 1991).

RESULTS

Interspecific Differences

Fan-Based Method: CVA-MANOVA analysis of the FB method revealed a single CV with significant differences between species (Bartlett's test, Wilk's $\Lambda = 0.0836$; $p < 0.01$; Fig. 3a). Based on Mahalanobis distances, all specimens (*Panopea generosa*, n = 30 and *P. globosa*, n = 108) were correctly assigned to species. The partial Procrustes DBM between the two spe-

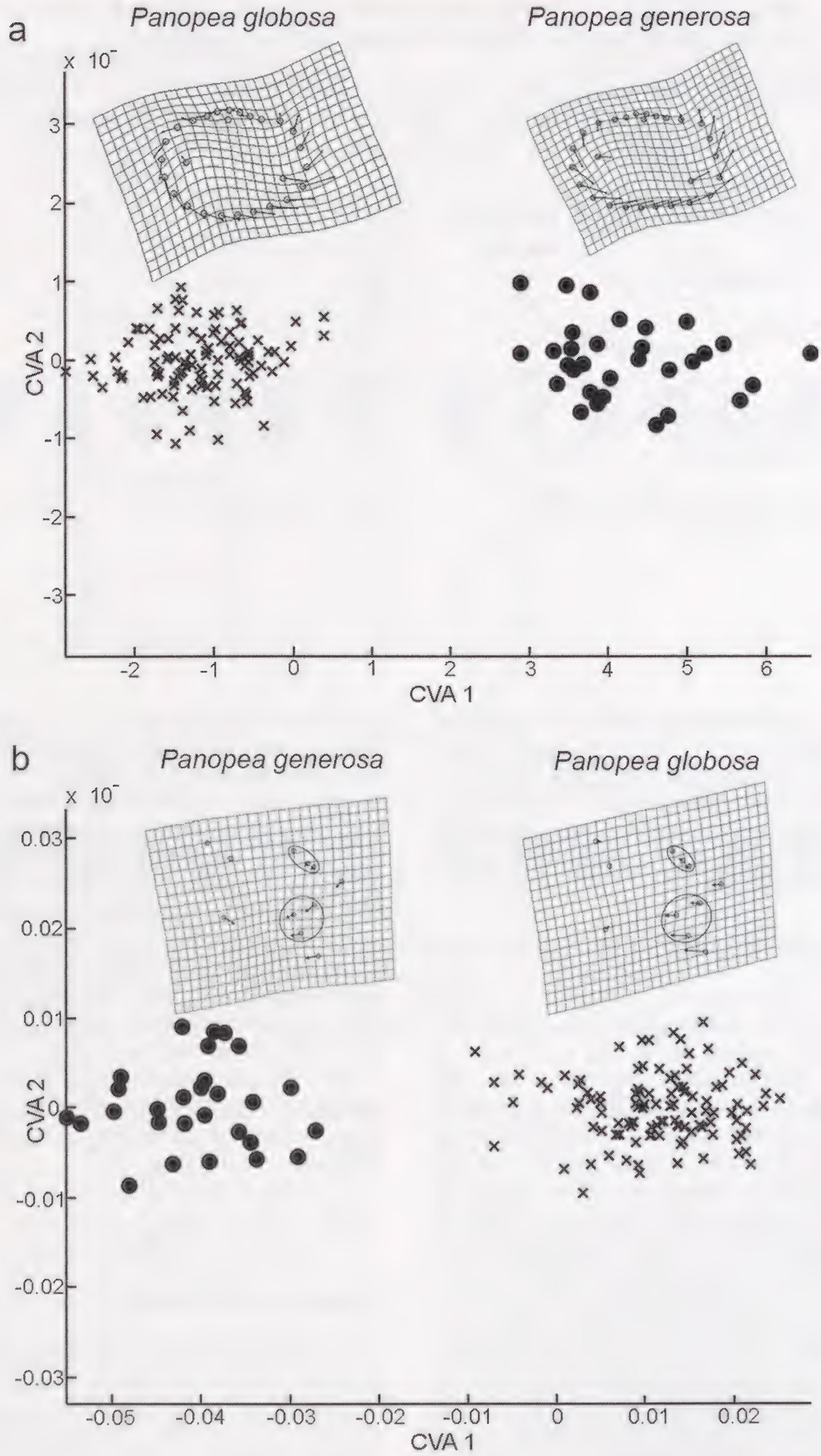

FIG. 3. Plot of interspecific canonical analyses of sets of variables and thin-plate spline with vectors of outline (a) and internal scars (b), nymph and pallial sinus, oval and circle respectively.

TABLE 3. Goodall's F-test and distances between means (DBM) of outline and internal landmarks in *Panopea globosa*. BM = Bahía Magdalena; GU = Guaymas; SF = San Felipe; PP = Puerto Peñasco. All comparisons were significant (P < 0.01).

	Comparison	F	DBM
Outline			
	BM vs GU	16.08	0.0475
	BM vs SF	6.25	0.0344
	BM vs PP	25.45	0.0589
	Gu vs SF	12.78	0.0440
	Guvs PP	14.94	0.0411
	SF vs PP	8.13	0.0342
Internal landmarks			
	BM vs GU	6.65	0.0540
	BM vs SF	6.35	0.0612
	BM vs PP	11.46	0.0702
	GU vs SF	7.90	0.0636
	GU vs PP	6.96	0.0517
	SF vs PP	2.69	0.0366

cies was significant (DBM = 0.065, Goodall's F-test with 900 bootstraps, F = 43.8, p = 0). The first two principal components (PC) accounted for 71% and 66% of the total variance in *P. generosa* and *P. globosa*, respectively (Table 2). Note that the loadings of all other PCs were less than 1%; they are not shown in Table 2, as they contribute little to the variance. In contrast, PC1 and PC2 fan rays contribute to most of the variance for the two species.

Inner Landmark-Based Method: CVA-MANOVA analysis of the ILB results revealed a single CV with significant differences between species (Bartlett's test, Wilk's $\Lambda = 0.0987$, $p < 0.01$; Fig. 3b). All *Panopea generosa* and *P. globosa* specimens were correctly assigned to species based on Mahalanobis distances. The partial Procrustes DBM of internal landmarks was significant (DBM = 0.0982, Goodall's F-test with 900 bootstraps, F = 32.72; p = 0). The first two PCs accounted for 58 and 45% of the total variance in *P. generosa* and *P. globosa*, respectively (Table 2).

When we compare the FB and ILB results, the thin plate splines of the first two PCs obtained by Procrustes superimposition of centroid size reveal easily perceivable shape differences in both the deformation grids and vector displacement (Fig. 3a, b).

TABLE 4. Intraspecific individual assigned with the Mahalanobis distance approach among groups of *Panopea globosa*. BM = Bahía Magdalena; GU = Guaymas; SF = San Felipe; PP = Puerto Peñasco.

		BM	GU	BM	GU
Outline					
	BM	30	0	0	0
	GU	2	28	0	0
	SF	0	0	18	0
	PP	0	1	0	29
Internal landmarks					
	BM	28	1	0	1
	GU	2	27	0	1
	SF	0	1	10	7
	PP	1	2	9	18

Intraspecific Differences

Fan-Based Method: Using the FB approach we observed three CVs of outline shape variation among *P. globosa* groups with CVA-MANOVA (Fig. 4a). Axis 1 (Wilk's $\Lambda = 0.0159$, $p < 0.01$) separated the Pacific group (Bahía Magdalena) from the Gulf of California groups (Guaymas, San Felipe, and Puerto Peñasco); Axis 2 (Wilk's $\Lambda = 0.0965$, $p < 0.01$) separated the southern Gulf group (Guaymas) from the northern Gulf groups (San Felipe and Puerto Peñasco); Axis 3 (Wilk's $\Lambda = 0.3620$, $p < 0.01$) placed San Felipe and Puerto Peñasco in the same group. Mahalanobis distances correctly assigned 100% of the specimens to the Bahía Magdalena and San Felipe groups. In contrast, correct allocation was slightly lower for the localities of Guaymas and Puerto Peñasco (93 and 97%, respectively). The first two PCs account for a high percentage of the total variance (58–71%) at all sites (Table 2). Goodall's F-test values and the partial Procrustes DBM among *P. globosa* groups outlines were significant (Table 3).

Inner Landmark-Based Method: When comparing shape variation among internal landmarks using the ILB approach in the same groups (Fig. 4b), we obtained two CVs: Axis 1 (Wilk's $\Lambda = 0.0800$, $p < 0.01$) discriminated the Pacific group (Bahía Magdalena) from the Gulf groups (Guaymas, San Felipe, and Puerto Peñasco), and Axis 2 (Wilk's $\Lambda = 0.3396$, p <

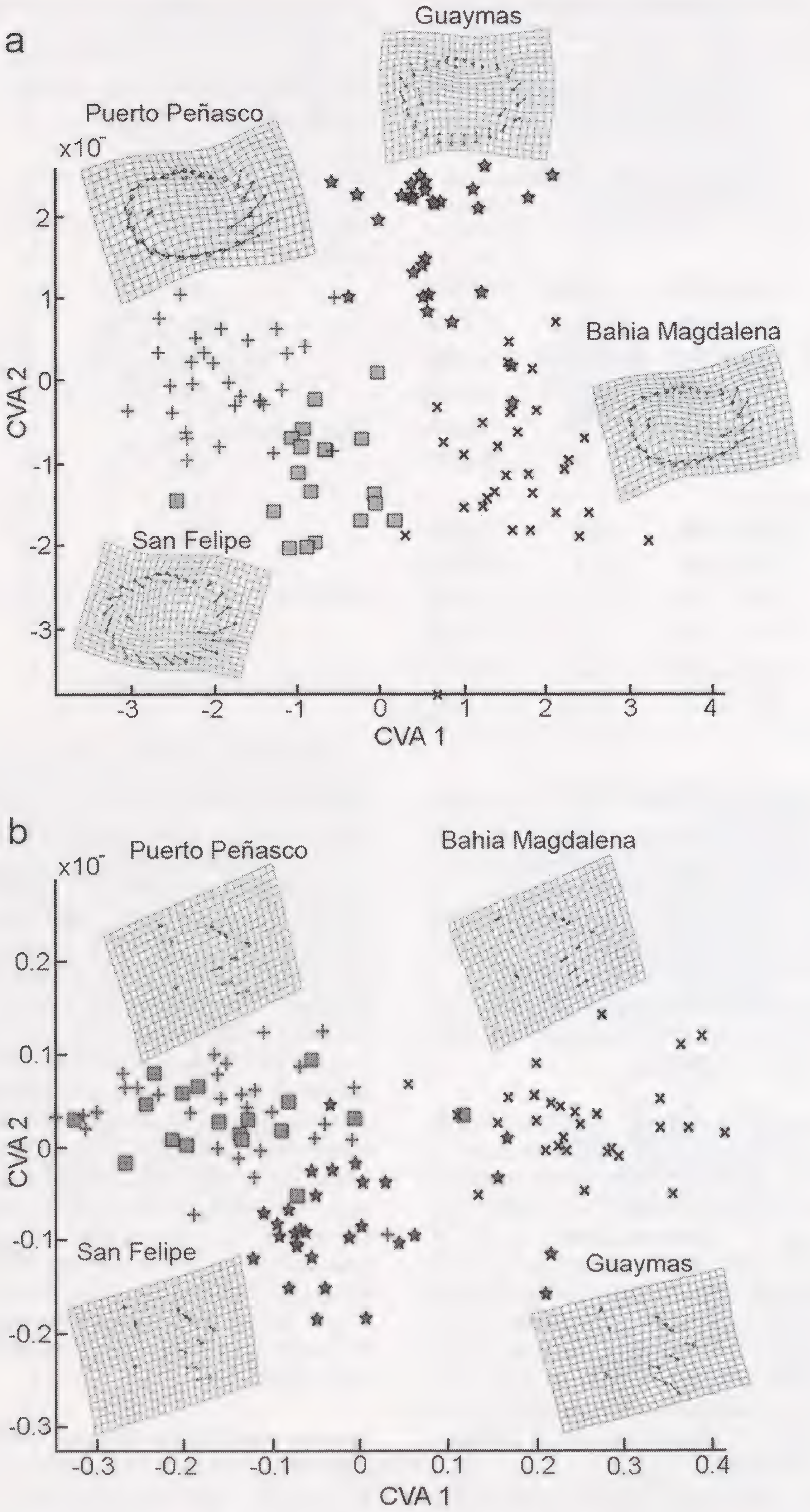

FIG. 4. Intraspecific canonical analyses of sets of variables plot of shell shape variation of *Panopea globosa* collections in northwest Mexico. Outline (a), internal scars (b).

0.01) included all Gulf groups. Group assignment with Mahalanobis distances revealed some incorrect assignments of northern Gulf geoducks: 37% of Puerto Peñasco specimens were grouped incorrectly with San Felipe, while 45% of the samples of San Felipe were incorrectly grouped with Puerto Peñasco. In contrast, > 90% of Bahía Magdalena and Guaymas specimens were correctly assigned (Table 4).

With these landmarks, the first two PCs accounted for 50–54% of the total variance (Table 2). Goodall's F-test values and DBM were also significant (Table 3). Thin plate splines revealed the greatest differences in vector length and displacement of landmarks 4–7 and 10 between Pacific *P. globosa* and the three Gulf groups (Fig. 4b).

DISCUSSION

In this study we used two methods to analyze interspecific and intraspecific phenotypic variation: a new proposed FB method, for external contours of the shell, as well as the more traditional ILB method for mapping the interior of the shells for geometric morphology analyses to determine interspecific shell shape differences in Mexican geoducks. Our results clearly delimited two groups that correspond to the two species, *Panopea generosa* and *P. globosa,* in agreement with the original descriptions (Gould, 1850; Dall, 1898). The specimens from Bahía Magdalena (Pacific coast) grouped with *P. globosa*, corroborating the traditional taxonomical procedure. The results indicate a much wider distribution for *P. globosa* than only the northern Gulf of California as previously reported (Coan et al., 2000; Briggs, 1974; Brusca, 1980; Hastings, 2000; Calderón-Aguilera et al., 2010; Rocha-Olivares et al., 2010).

Interspecific Shell Shape Variation

Prior studies using traditional morphometric analyses have shown notable shape differences between *Panopea generosa* and *P. globosa* (Rocha-Olivares et al., 2010). Using three linear measurements, these authors found that *P. generosa* had a more homogeneous shell length compared to *P. globosa* and they successfully discriminated the two species. The present study corroborates this finding and increases the resolution of inter-specific morphological shell variation.

The ILB method has been used to determine shell shape variation in other bivalves. For example, Innes & Bates (1999) determined contour differences between *Mytilus edulis* and *M. trossulus* (Wilk's $\Lambda = 0.625$), whereas Roopnarine & Vermeij (2000) reported Wilk's $\Lambda = 0.25$ for internal shape variation between *Chione cancellata* and *C. elevata*. In contrast, in our study Bartlett's test was highly discriminant between the two *Panopea* species (Wilk's $\Lambda = 0.08$ and 0.09 for FB and ILB, respectively).

The consensus outline shape of *Panopea globosa* is more inflated, with a narrower posterior end compared to *P. generosa*. The umbo in *P. globosa* is near the posterior end, while more centrally located in *P. generosa*. The off-center placement of the umbo in *P. globosa* may be related to an anatomical adaptation which aids in maintaining valve gape due the more inflated shell; Savazzi (1987) discusses the hypothesized relationship between shell inflation and umbo displacement, and Ubukata (2003) observed in pteroids a tendency of shell extension in the antero-ventral direction.

In our study, variation in the inner shell indicates that *Panopea globosa* has a shorter nymph and smaller ligament (landmarks 1–3), but a deeper pallial sinus than *P. generosa* (landmarks 4–6). Stanley (1970, 1979) and Lockwood (2004) describe the pallial sinus as the space where siphonate bivalves contract the siphon. Kondo (1987) suggested that the ratio of pallial sinus depth to shell length is closely correlated to the maximum burrowing depth. Although we found a deeper pallial sinus in *P. globosa* than in *P. generosa,* we did not measure syphon length or burrowing depth thus we are unable to corroborate Kondo´s hypothesis.

The FB and ILB methods showed that the first two PCs in *Panopea generosa* accounted for more variability in shell shape than in *P. globosa* (Table 2). To fully corroborate these results in a future study, it will be necessary to examine specimens of *P. generosa* from other sites.

Panopea globosa Intraspecific Shell Shape Variation

Both the FB and ILB methods revealed that *P. globosa* of Bahía Magdalena are morphologically distinct from the three other localities of the Gulf of California. Nevertheless, the FB method more clearly distinguished three different groups, while the more traditional ILB method exhibited lower fidelity since it was only able to distinguish two groups.

Our results suggest a shell shape adaptation or phenotypic response to environmental conditions at each site. The intraspecific CVA analyses reveal significant differences among *Panopea globosa* sites, where Pacific *P. globosa* (Bahía Magdalena) have more elongated shells but a shorter pallial sinus than those in the Gulf of California. Moreover, within the Gulf, our analyses revealed that Guaymas geoducks are smaller and have a more inflated shell and deeper pallial sinus compared to those from San Felipe and Puerto Peñasco. Rocha-Olivares et al. (2010) also reported similar size differences between *P. globosa* from the upper and middle Gulf.

Shape differences might also be explained by genetic differences, as observed in pectinids from the Pacific and Gulf sides of the Baja California Peninsula (Cruz & Ibarra, 1997; Cruz et al., 1998), or by phenotypic plasticity noted in other bivalve populations subjected to different environmental conditions (Palmer et al., 2004; Krapivka et al., 2007; Costa et al., 2008a; Elliot et al., 2008; Sokolowski et al., 2008; Márquez et al., 2010). In addition, morphological polymorphisms may result from gene-environment interactions (Rawson & Hilbish, 1991; Trapani, 2003). The variation in *P. globosa* we observed suggests either phenotypic plasticity or local adaptation due to gene-environment interaction.

Shell shape differences between Bahía Magdalena and Gulf of California geoducks might be associated with temperate environmental conditions, in contrast to the northern Gulf, which is a warm-temperate region (Lluch-Belda et al., 2000; Calderón-Aguilera et al., 2010). On the other hand, the lower shape differentiation between San Felipe and Puerto Peñasco might be caused by gene flow due to geographical proximity and circulation patterns, since the anticyclonic circulation during November-April in the northern Gulf (Lavín & Marinone, 2003) exactly overlaps with the reproductive period for *P. globosa* (Calderón-Aguilera et al., 2010).

The notable shell shape differences of *Panopea globosa* in Guaymas may be due to drastically higher temperatures conditions during the summer months (Lluch-Cota & Arias, 2000; Green et al., 2005); the most abundant beds on this site are located in shallower waters (8–12 m, Aragón-Noriega et al., 2007, Rocha-Olivares et al., 2010) compared with the other studied localities (Bahía Magdalena 10–20 m, González-Peláez Centro de Investigaciones Biológicas del Noroeste, México 2010, pers. comm.; San Felipe, Puerto Peñasco 10–25 m, Rocha-Olivares et al., 2010). In addition, primary productivity is lower in Guaymas since there are essentially no currents most of the year (Lluch-Cota & Arias, 2000; Green et al., 2005).

The novel FB method of contours was found to have higher resolution than the traditional ILB method for distinguishing intraspecific phenotypic differences among the three *Panopea globosa* groupings: (1) Bahía Magdalena; (2) San Felipe-Puerto Peñasco; and (3) Guaymas. Geometric morphometric analyses suggest the possibility of geographic and breeding isolation between *P. globosa* of Bahía Magdalena in the Pacific and their conspecifics from the Gulf of California. Genetic studies are underway to understand the evolutionary history of *P. generosa* and *P. globosa* and the genetic relationships among populations of *P. globosa*.

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